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FACTORS INFLUENCING GROWTH AND SURVIVAL OF WHITE SUCKER, *Catostomus commersoni*

by

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The ultimate upper incipient lethal temperature (UUILT), determined by slowly increasing (0.5°C/day) acclimation temperature to death, was 32.5°C for juvenile white suckers and 31.5°C for adults. The UUILT was 2-3°C higher than the upper lethal temperatures measured by the classical approach involving the direct transfer technique.

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SECTION 1

INTRODUCTION

Growth of fish is affected by many variables including temperature, season, body size, and food quality and quantity. These factors influencing growth have been investigated with various species of salmonids (Brown 1946; Brett et al. 1969; Brett 1971 a, b; Shelbourn et al. 1973; Brett and Shelbourn 1975; Elliot 1975; Wurtsbaugh and Davis 1977). No studies have described the thermal responsiveness of cool- and warm-water species throughout an annual growth cycle.

The white sucker, Catostomus commersoni, is a widespread cool-water species important as a forage and bait fish. Both growth response as well as lethal limits are necessary criteria to identify thermal impact on the environment, to improve culture techniques for laboratory research and to enhance the bait industry. McCormick et al. (1977) have shown that sucker fry grow best at a temperature of 26.9°C and reported an upper incipient lethal temperature of 30.5°C for swim-up larvae acclimated to 21.1°C. Brett (1944) reported an ultimate upper incipient lethal temperature of 31.2°C for juvenile white suckers using a direct transfer technique from an acclimation temperature of 25°C. Hart (1947) indicated that the ultimate upper lethal temperature for juvenile suckers was 29.3°C. Hokanson (1977) noted that the upper incipient lethal temperature of a species may vary as much as 4°C. Highest values of the ultimate upper incipient lethal temperatures occurred for summer tests at the highest acclimation temperature increasing slowly to

the lethal temperature.

The purpose of the present study was to investigate the growth and mortality rates of juvenile and adult white sucker under different temperature regimens as related to body size, season, daylength and ration level. Preliminary studies were conducted to determine conditions that maximize growth prior to initiation of experimental studies. The upper lethal temperatures of suckers of different sizes were estimated by the direct transfer method and by slowly raising the acclimation temperature 0.5^{o}C/day until death occurred.

SECTION 2

CONCLUSIONS AND RECOMMENDATIONS

The growth optimum and ultimate upper incipient lethal temperature (UUILT) of a species are parameters used in derivation of summer temperature criteria for aquatic life. The growth optimum varied from 19-26^{o}C for juvenile white suckers while the UUILT varied from 28.2 to 32.5^{o}C depending on experimental conditions.

Growth of fish was best when reared without any discernible current flow.

Growth of fish reared under shaded conditions was increased by an average of 43% over those reared under unshaded conditions.

Maximum growth was observed at 25^{o}C on excess rations (9.11% fish body dry weight) and at 19^{o}C on restricted rations (1.5%). Best growth was observed with live tubificid worms presented over a natural sand substrate. Growth on various diets decreased in the following order: Tubificids (sand substrate) >Tubificids (no soil substrate) >frozen Daphnia >Oregon Moist pellets >Glencoe Mills pellets. Maximum gross food conversion efficiency was 26% at 22^{o}C and 3.0% ration level of tubificids.

Maximum specific growth rate decreased nearly 4-fold over a size range of 12 to 175g. Optimum temperature for growth was not influenced over this size range. The weight exponent (slope) for this size range was -0.45 which decreased when smaller fish were included in the growth rate-body weight relationship.

Fish of a common size had a 2-fold increase in maximum growth rate in spring compared to other seasons. There was no difference in growth rate between summer and winter fish under a 15hL-9hD photoperiod. Maximum growth in summer occurred at 26°C and at 24°C in winter and spring tests.

Daylength changes had no significant effect on maximum growth rate or optimum temperature. However, attainment of maximum growth under test conditions was increased from 2 to 4 weeks when fish were reared under 15hL-9hD and 9hL-15hD photoperiods, respectively, in a winter test.

The highest UUILT (32.5°C) was achieved by slowly raising the test temperature 0.5°C/day until death. This approach measured an UUILT that was 2-3°C higher than that measured by the classical approach involving the direct transfer of fish from an acclimation temperature to a series of lethal levels.

The UUILT for newly hatched larvae, swim-up larvae, juvenile, and adults were 28.2, 30.5, 32.5, and 31.5°C, respectively.

It is recommended that each investigator run a series of preliminary tests to optimize culture conditions prior to measurement of the physiological optima for each respective species. Better control of light intensity in bioassays with nocturnal or deep-water organisms is especially encouraged.

Growth of white suckers on live tubificids should be compared to growth on natural components in their diet including live Cladocera and macroinvertebrates.

Future bioenergetic studies should cover a broader biokinetic range of temperatures to include the lower and upper limits of zero net growth.

The large variation in measurement of the physiological optima and UUILT for one species herein suggests that temperature criteria data base be critically appraised or revised before adaptation of any literature values

to field problems (ie. 316a demonstrations).

Field validation of the laboratory data base on temperature criteria is needed to confirm the best test procedures.

SECTION 3

MATERIALS AND METHODS

EXPERIMENTAL TANKS AND WATER SUPPLY

All tests were conducted in 210 x 54 x 54 cm fiberglass tanks where a 30 cm standpipe at the downstream end of the tank maintained a volume of 340 liters. The water in each experimental tank, representing one test temperature, was supplied by its own head tank where dissolved oxygen and temperature were regulated. Water temperature in the head tank was regulated by either electrical immersion heaters as used by Smith and Koenst (1975) or a thermostatically controlled solenoid valve which allowed hot water to flow through a series of immersed stainless steel heating coils. Dissolved oxygen concentration was maintained near air saturation in the head tanks with the aid of airstones. An airstone also was placed in each experimental fish tank to increase the oxygen concentration and to prevent thermal statification. Water flowed by gravity from the head tank through garden hose to a horizontally placed polyvinyl chloride pipe with three constricted glass outlet tubes placed equally apart above the tank. These glass tubes dispensed a continuous flow of water into the fish tank at a rate of 1.8-2.0 1/min. The water supply was from a deep well and was transported to the head tanks through polyvinyl chloride pipe. A comprehensive analysis of the well water was reported by Smith et al. (1976). Temperature was measured daily with an immersion thermomemter graduated to 0.1^{o}C. A 24-channel temperature recorder monitored temperature variation at less precise levels. Daylength was maintained at a

15h light-9h dark photoperiod during acclimation and testing unless otherwise stated. Dissolved oxygen was measured twice weekly with the azide modification of the Winkler method (APHA et al. 1971). Total alkalinity was determined twice during each test. A weekly determination of pH was made with a pH meter. Temperatures fluctuated slightly (standard deviations ranged from 0.04 to 0.12); pH ranged from 8.18 to 8.30; dissolved oxygen ranged between 78-92% air saturation; and total alkalinity averaged 235 mg/l as $CaCO_3$.

EXPERIMENTAL FISH

All juvenile suckers were acquired from a bait dealer in Sherburne County, Minnesota. Large juvenile suckers (140-200 g) were secured from the same source, but after they had been maintained for one year in the ambient temperature study channels of the Monticello Ecological Research Station, U.S. Environmental Protection Agency, Monticello, Minnesota. Adult suckers (1000 g) were collected from Greenwood Lake, Cook County, Minnesota. Upon arrival at the University of Minnesota Fisheries Laboratory, all fish were given a routine prophylactic treatment of formalin plus malachite green oxalate for 3 days as prescribed by the Committee on Methods for Toxicity Tests with Aquatic Organisms (1975). Fish were kept in holding tanks at 11°C prior to acclimation.

FISH FOOD

Several types of food were given to the fish during holding and testing. During the initial holding period, fish were fed frozen adult brine shrimp (Artemia) and Oregon Moist pellets. Different types of food were presented to the suckers during the acclimation and testing period. During the initial 18 months of the study, Oregon Moist pellets (3/64) was primarily used for growth tests. During the second phase, live tubificid worms were fed to the

fish. Along with the food previously mentioned, Glencoe pellets (#1 granules) and frozen adult Daphnia magna were also used in the specific food test.

An excess ration of Oregon Moist pellets was fed to the fish with the aid of an automatic clock feeder. This method was useful in presenting the food continuously over a long period of time and especially in dispensing the food at night during the white suckers' natural active feeding period.

Tubificid worms were collected from two sources: Raven Creek, Scott County, Minnesota, and in a trout hatchery. They were held in a holding tank with clean substrate and flowing water for several weeks prior to being fed to the fish. Subsamples of worms were analyzed for body constituents and were found to contain about 76% water, 7% fat, and 13% protein. Live worms were placed in the fish tanks and, thus, were available for feeding 24 hours per day. A fine granular sand substrate (1.5 cm deep) was placed in each experimental tank to aid in the acceptance of tubificids as a food.

Daphnia were captured in Raven Creek, Scott County, Minnesota, which was fed by an outfall from a sewage treatment pond. Daphnia were in abundance during May and June and large amounts were collected with drift nets in a short time. They were immediately frozen with dry ice at capture and were kept frozen until fed to the fish. Daphnia cubes were thawed and presented to the fish at least twice daily.

PROXIMATE ANALYSIS

Half of the fish were frozen at the end of each experiment for determination of fat and protein content. Water content was determined from fresh fish after each test and from frozen fish at a later date. Fish were oven-dried at 105^{o}C for 24h to determine percentage water content. Fat content was determined from frozen samples which were oven-dried at 85^{o}C to a constant

weight. The dried samples were crushed and extracted with n-hexane (Brett et al. 1969). The residue remaining after fat-extraction was analyzed for nitrogen content by the micro-Kjeldahl technique for protein determination. A factor of 6.25 was used to obtain the mean protein value. Subsamples of tubificid worms were also analyzed for body constituents with the same procedures.

EXPERIMENTAL PROCEDURES

Generalized procedures are described herein. Specific details of the experimental design of each study will be described under the appropriate section.

All fish were transferred from holding tanks to experimental tanks within a period of 7 days after prophylactic treatment. Fish were randomly assigned to a test tank after screening for a relatively uniform size. The temperature was increased at a rate of $1^{o}C$/day, and the fish were given an additional acclimation period of 2 weeks to experimental tanks after the final test temperature was reached.

To start the growth test, all fish were anesthetized with tricaine methanesulfonate (MS-222) and cold-branded with "liquid nitrogen". The branding was done with branding irons that were super cooled within a liquid nitrogen bath. The numerical brand was placed dorsally above the base of the pectoral fin. Fish were blotted with paper towels and weighed to the nearest 0.01 g and measured to the nearest mm during the marking procedures, and every 2 weeks throughout a 4- to 6-week growth period. Fish were fed daily during acclimation and testing, and observations were made for mortality. Growth in 2-week intervals was expressed as a specific rate (percent change in weight/time) after Brett et al. (1969). The specific growth rate is the slope of the

regression of the natural log of weight on time multiplied by 100. All data were statistically examined to describe the optimum range by Analysis of Variance followed by Duncan's New Multiple Range Test (Steele and Torrie 1960). The data was reported as specific growth rate $\pm$ 2 standard errors.

The upper incipient lethal temperature (UILT) was determined by the method of Fry (1947) whereby fish were transferred directly from a constant acclimation temperature to a series of constant temperature baths bracketing the median response. The incipient lethal temperature was defined by Fry as the temperature beyond which 50 percent of the population cannot live for an indefinite period of time. The UILT was established for acclimation temperatures of 12, 16, 20, and 24^{o} C as an initial range finding test. The ultimate upper incipient lethal temperature (UUILT) is the highest UILT which can be raised by thermal acclimation. The UUILT was determined by exposing acclimated fish to a slow temperature rise (0.5^{o}C/day) until death after Cocking (1959) and Fry (1971). Percent survival and the corresponding mean daily temperature in the preceeding and final 24h interval was used to determine the temperature where 50 percent of the population would die by graphical interpolation. The UUILT was determined for white suckers of different sizes after a 4-week growth study for fish reared at constant temperatures near optimum (26 and 28 ^{o}C). Feeding was terminated above 30^{o}C since it could influence the response to the upper lethal temperature.

SECTION 4

FACTORS INFLUENCING GROWTH

PRELIMINARY OBSERVATIONS

During the first phase of the project, it became apparent that the white sucker would not achieve maximum growth in the laboratory using methods that have been previously demonstrated with other fish species. It was hypothesized that sucker growth could be maximized by controlling variables such as water current flow, temperature, light intensity, and diet quality. These variables can maximize sucker growth by influencing food acceptance and/or reducing their spontaneous activity and routine metabolism.

Water Current

Juvenile suckers placed in holding tanks did not readily accept pellet food (Oregon Moist) but did feed readily on adult frozen brine shrimp. The brine shrimp distributed more evenly in the tanks due to slight currents created by airstones and the fresh water inflow. A test was initiated to determine if current would enhance food acceptance. Water was circulated by a pump in a circular tank to achieve the desired current. Fish were tested under low light intensity (less than 5 ft-candles) at 22^{o}C under both current and non-current conditions. Fish living without water current grew nearly twice the rate of fish living in a current (Table 1).

Temperature

A preliminary test was conducted to determine the optimum temperature for

TABLE 1. EFFECT OF CURRENT FLOW ON GROWTH OF WHITE SUCKERS*

	$\bar{x}$ Initial wet wt. (g)	Specific growth rate (%/day)
Current+	11.2	0.938
Non-current++	10.2	1.839

*Test conducted in summer at 22°C under a light intensity of less than 5 ft-candles. All fish fed an excess ration of Oregon Moist pellets.

+Water current was created by a pump in a circular tank to disperse food pellets and transport them to fish. Flow rate and velocity was not measured.

++Fish received a similar continuous flow of fresh water, but flow was adjusted to avoid creating any discernible current.

growth of white suckers fed to satiation on Oregon Moist pellets. A growth test was started with juvenile suckers (10 g) at eight different temperatures ranging from 12° to 29°C (Table 2). Fish grew best at 24°C and had an optimum temperature range of 20° to 26°C. Growth was significantly reduced above and below this temperature range ($P < 0.05$).

Light Intensity

The current (Table 1) and temperature (Table 2) experiments indicate that light intensity could be an important factor influencing growth. A comparison of growth rates at 22°C between the two types of tests indicate that suckers grew at a greater rate at low light intensity. It was observed by Stewart (1926) and Campbell (1971) that white suckers normally feed during darkness. Nocturnal activity was also noted by Spoor and Schloemer (1938) who found suckers to move inshore during evening hours and offshore during morning hours. A growth test with 35 g suckers was initiated to investigate the effect of

TABLE 2. EFFECT OF TEMPERATURE ON GROWTH RATE OF WHITE SUCKERS*

Temperature (C)	$\bar{x}$ Initial wet wt. (g)	Specific growth rate (%/day)+
11.9	10.72	0.140 ± 0.051
16.0	11.01	0.330 ± 0.122
18.0	10.74	0.669 ± 0.195
19.9	10.93	1.014 ± 0.223
22.0	10.93	1.032 ± 0.206
24.0	10.63	1.070 ± 0.200
26.0	10.41	0.931 ± 0.187
28.9	9.91	-0.032 ± 0.332

*Tests conducted during fall at a light intensity of 11.5 ft-candles. Fish fed an excess ration of Oregon Moist pellets over a 42-day period.

+Rate ± 2 SE; N = 20 for each treatment.

light intensity. After a two-week acclimation period to test conditions, fish were tested for growth for a two-week period under unshaded conditions (11.5 ft-candles). This was followed by a two-week growth period where shade was provided by placement of a black plastic cover over the lower two-thirds of the water surface. Light was supplied by two 40-watt fluorescent bulbs (Vita-Lite) providing a light intensity of 11.5 ft-candles in the unshaded portion and 0 ft-candles in the shaded portion. Fish were always observed at the lowest light intensity. Fish were tested at seven different temperatures ranging from 14° to 26°C (Table 3). For all temperatures combined, growth rate was increased by an average of 43% after shade was provided, even though these fish were a larger initial size than in the unshaded test. Growth rate was significantly greater under shaded conditions ($P < 0.05$). The unshaded test showed 22°C to be the optimum temperature for growth as compared to all other temperatures ($P < 0.05$), while the shaded test showed an optimum temperature of 24°C and an optimum temperature range of 18°C to 26°C ($P < 0.05$).

TABLE 3. GROWTH RATE OF WHITE SUCKERS AT DIFFERENT TEMPERATURES AND LIGHT INTENSITIES*

Temperature (C)	$\bar{x}$ Initial wet wt. (g)	Specific growth rate (%/day)+	
		Unshaded++	Shaded+++
14.0	37.48	0.34 ± 0.14	0.63 ± 0.26
16.0	35.30	0.52 ± 0.20	0.73 ± 0.21
18.0	34.28	0.67 ± 0.22	1.05 ± 0.27
20.0	35.39	0.79 ± 0.23	0.82 ± 0.24
21.9	34.19	1.22 ± 0.31	1.40 ± 0.35
24.0	34.43	0.87 ± 0.28	1.48 ± 0.34
26.0	33.57	0.87 ± 0.17	1.13 ± 0.26

*Fish tested in winter and fed an excess ration of Oregon Moist pellets.

+Rate ± 2 SE for N = 10 for each treatment.

++11.5 ft-candles.

+++0 ft-candles underneath shaded portion of tank (lower two-thirds area), and 11.5 ft-candles at upper end (one-third area).

Eisler (1957) concluded that high light conditions stimulated growth of chinook salmon fry. Conversely, suckers are nocturnal feeders and could be stimulated by low light conditions.

Diet Quality

It was thought food type could still be a significant limiting factor in achieving maximum growth rate (Brett 1971b). Furthermore, the amount of Oregon Moist consumed by the suckers would be difficult to quantify over time. Live food would be preferable in food ration tests. Tests were conducted to determine food type most suitable in obtaining maximum growth rates. The presence of a substrate with live food was also tested as a factor influencing growth or food acceptability. Juvenile suckers were tested for a two-week growth period at 22°C after a two-week acclimation period. Foods tested were

TABLE 4. GROWTH OF WHITE SUCKERS AFFECTED BY DIET QUALITY*

Food	Specific growth rate (%/day)
Live tubificid worms (sand substrate)+	4.33
Live tubificid worms (no substrate)	3.30
Frozen Daphnia	3.19
Oregon Moist	1.78
Glencoe Mills	-0.03

*Test conducted in spring at low light intensity (0 ft-candles under lower two-thirds tank) at 22°C. Initial wet weight was 10-11 g.

+A 1.5 cm layer of fine sand distributed evenly over bottom of tank.

Oregon Moist pellets, Glencoe pellets, frozen adult Daphnia and tubificid worms. The tubificids were presented as two treatments, one being a tank with no substrate and the other being a tank with a sand bottom. All fish were fed to satiation. Fish fed live tubificids over a sand substrate had a maximum growth rate of 4.3%/day (Table 4). Growth declined in decreasing order from tubificids (sand substrate) > tubificids (no soil substrate) > frozen Daphnia > Oregon Moist > Glencoe Mills.

As a result of the preliminary tests, culture techniques enhancing growth were incorporated into subsequent experimental procedures. All experiments were conducted under low light intensity (11.5 ft-candles at upper one-third tank; 0 ft-candles under shade cover over lower two-thirds tank), fish were fed live tubificid worms, and a sand substrate was provided for feeding. A continuous flow-through (1.8-2.0 l/min) with no current was provided in the test chambers. These improvements in sucker culture increased growth rates

TABLE 5. EFFECT OF TEMPERATURE AND BODY SIZE ON GROWTH OF WHITE SUCKERS*

$\bar{x}$ Initial wet wt. (g)	N	Temperature	Specific growth rate (%/day)+
11.79	10	12.1	0.05 ± 0.05
10.79	10	17.0	0.55 ± 0.22
11.73	10	20.9	1.79 ± 0.25
10.71	10	24.0	1.80 ± 0.30
12.61	10	25.9	2.37 ± 0.27
12.29	10	28.1	1.33 ± 0.39
11.96	10	29.9	0.20 ± 0.21
166.39	5	12.1	0.40 ± 0.08
161.54	5	17.0	0.08 ± 0.06
172.96	5	21.0	0.54 ± 0.08
161.67	5	24.0	0.65 ± 0.15
175.06	5	26.1	0.68 ± 0.14
157.31	5	28.0	0.24 ± 0.09

*A summer test at low light intensity. Fish fed an excess of live tubificid worms.

+Rate ± 2 SE.

more than four-fold to a level that approximates growth rates observed under field conditions at low fish density (K.E.F. Hokanson, U.S. EPA, Monticello MN, personal communication). Mortality of fish was also negligible at all temperatures herein when growth conditions were optimized.

TEMPERATURE X BODY SIZE

The effect of body size of white suckers on growth rates were tested at excess rations of live tubificid worms at different temperatures during the summer. Two sizes of juvenile white suckers were tested (Table 5). Fish of both sizes showed an optimum temperature range for growth to be 21-26^{o}C ($P < 0.05$). Maximum growth occurred at 26^{o}C where the 12.6 g fish grew at a rate of 2.37%/day and the 175.1 g fish grew 0.68%/day. Juvenile suckers (mean wet wt. 25.6 g) tested at excess rations at 25^{o}C grew at a maximum rate of 1.38%/day (see Ration Size X Temperature section, Table 8).

Brett and Shelbourn (1975) found that a log-log transformation provides a good linear relationship between maximum growth rate and body weight for salmonids. A similar relationship exists for juvenile white suckers (Fig. 1). The maximum growth rate relationship for white suckers fed excess rations at 26°C for a weight range of 12.6-175.1 g was expressed by the linearized equation:

$$\ln G = 1.9160 - 0.4523 \ln W \quad (1)$$

where G = specific growth rate (%/day)

W = initial wet weight (g)

The fitted regression line between the summer data points had an R^2 value of 0.967.

Suckers tested in the springtime showed a higher growth rate than at other seasons for similar sized fish (see Season X Daylength section, Table 6). The maximum growth rate - body weight relationship (10.1-53.6 g) was derived only for comparative purposes by the linearized equation:

$$\ln G = 2.3541 - 0.3391 \ln W \quad (2)$$

Caution should be exercised in extrapolation of these data beyond the indicated size range as inclusion of smaller fish will reduce the size correction factor (slope) further. McCormick et al. (1977) observed a maximum specific growth rate of 14.8%/day for white sucker larvae with an initial wet weight of 4.1 mg. Addition of this data point to the spring growth rate-body weight relationship would give a slope of -0.168 with an $R^2 = 0.972$.

SEASON X DAYLENGTH

The effect of season and daylength on sucker growth was investigated. Fish were compared for growth at three different times of the year (spring, summer, and winter) and at three different temperatures (24, 26, and 28C) at

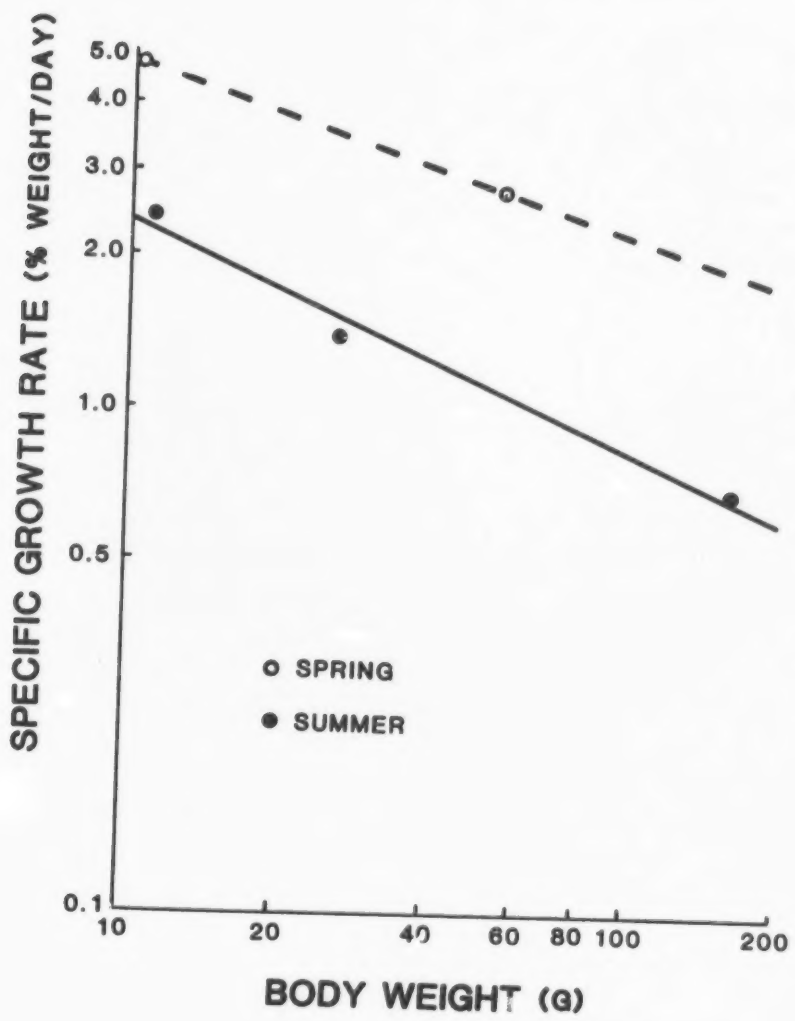

Figure 1. The relationship between initial body size and maximum growth rate of white suckers in the spring and summer.

at a 15h L-9h D photoperiod. Because of a possible effect of season and daylength on growth rate, winter fish were tested at two photoperiods: 15h L-9h D, and 9h L-15h D.

The time of year had a marked effect on growth rates of suckers. Fish during late spring (May-June) displayed nearly a two-fold increase in growth

TABLE 6. EFFECT OF SEASON AND DAYLENGTH ON MAXIMUM GROWTH OF JUVENILE WHITE SUCKERS AT THREE PRESCRIBED TEMPERATURES*

Season	Photoperiod h-L/h-D	$\bar{x}$ Initial wet wt. (g)	Temperature (C)	Specific growth rate (%/day)+
	15/9	10.14	24.0	4.80 ± 0.41
	15/9	9.97	26.0	4.35 ± 0.43
Spring++	15/9	9.50	28.0	2.89 ± 0.34
	15/9	53.56	24.0	2.73 ± 0.22
	15/9	55.00	26.1	2.60 ± 0.18
	15/9	51.47	28.0	1.66 ± 0.26
	15/9	10.71	24.0	1.80 ± 0.30
Summer++	15/9	12.61	25.9	2.37 ± 0.27
	15/9	12.29	28.1	1.33 ± 0.39
	15/9	11.66	24.0	2.39 ± 0.26
	15/9	11.17	26.0	2.33 ± 0.22
Winter++	15/9	11.17	28.0	1.67 ± 0.34
	9/15	12.13	24.1	2.71 ± 0.29
	9/15	11.41	26.0	2.60 ± 0.28
	9/15	11.40	27.9	1.78 ± 0.24

*Fish fed an excess ration of live tubificid worms at low light intensity.

+Rate ± 2 SE for N = 20.

++28 day growth test began in late May, late July, and early January, respectively.

rate compared to growth during summer and winter (Table 6, Fig. 1). Large juvenile suckers (54 g) displayed a greater growth rate (2.73%/day at 24°C) in the spring than did smaller 11 g individuals (1.80%/day at 24°C) in the summer. The optimum temperature for growth on excess rations was 26°C in summer and was reduced to 24°C in winter and spring tests, although growth rates were not significantly different ($P > 0.05$). Fish (10-12 g) showed no significant differences in growth rate between summer and winter seasons for a 15h L-9h D photoperiod.

One phenomenon brought out by the winter test was that photoperiod played an important part in the acclimation rate to test conditions based on

TABLE 7. EFFECT OF PHOTOPERIOD AND TEMPERATURE ON GROWTH STANZAS OF WHITE SUCKERS*

Temperature (C)	Specific growth rates (%/day)			
	Photoperiod			
	15h L - 9h D		9h L - 15h D	
	I+	II++	I	II
24	2.37	2.40	1.46	2.71
26	2.34	2.33	1.85	2.60
28	1.74	1.59	1.14	1.78

*Fish fed an excess of live tubificid worms at low light intensity in winter.

+Period I - first two-week period of growth test, following an initial 12-day acclimation period to test tanks, temperature, and photoperiod.

++Period II - second two-week period of growth test.

maximum growth potential. All fish prior to acclimation and testing were treated alike and were exposed to a short daylength during holding. Upon placement in their respective tanks, the photoperiod was changed over a period of three days, fish were acclimated to test temperatures at a rate of $1^{o}C$/day, and held for two weeks before the growth test began.

Results showed that fish acclimated to their test conditions at a slower rate when exposed to decreased daylight (Table 7). Based on maximum growth rate, it took over four weeks for the fish to be fully acclimated to their test conditions during shorter daylength hours compared to two weeks acclimation at the longer daylength. No differences in growth rates were noted between the first two weeks and the second two weeks of the 15h L-9h D photoperiod ($P > 0.05$). Conversely, suckers exposed to the 9h L-15h D photoperiod showed nearly a two-fold increase in growth between Period I and II ($P < 0.05$),

Although no significant differences in growth rates were found due to photoperiod based on the last two weeks of the test ($P > 0.05$), there was a large difference in growth rate between suckers exposed to the two photoperiods for the first two weeks of the test ($P < 0.05$). Special precautions are needed to insure complete acclimation to test conditions if "aseasonal" growth studies are to be conducted in winter.

RATION SIZE X TEMPERATURE

Growth tests were conducted on white suckers (mean wet wt. 29 g) at different temperatures and reduced ration levels of live tubificid worms. Fish were tested at five different temperatures (16, 19, 22, 25, and 28^{o}C) and five daily ration levels (0, 1.5, 3.0, 4.5%, and excess). The restricted ration was prescribed at the start of each two-week growth period and was based on estimated mean dry weights of fish at the mid-point of each interval. Mean dry weight was estimated from final weight (initial weight of current interval) and specific growth rate in the previous two-week interval). Subsequently, fish received a slightly higher portion of feed than the prescribed ration in the first week and a slightly lower portion in the latter week of the growth interval. Tubifex were weighed wet and fed daily to the fish. Subsamples of tubificid worms and fish were dried and weighed at the end of the study. Measured specific growth rates were used to estimate daily mean fish wet weights. These estimated fish wet weights and measured food wet weights were converted to dry weights to determine actual ration size per day. These measured ration sizes, test temperatures, and corresponding growth rates are reported in Table 8. Fish at 16^{o}C did not consume their prescribed ration of 1.5% equally. Because half of the fish consumed little food, the mean growth rate (0.047%/day) was lower than expected while feeding fish grew at

TABLE 8. THE EFFECT OF TEMPERATURE AND RATION SIZE ON GROWTH AND FOOD CONVERSION EFFICIENCIES OF THE WHITE SUCKER*

Temperature (C)	Ration sizes (% dry wt. food/ dry wt. fish/ day)	$\bar{x}$ Initial wet wt. (g)	Specific growth rate (%/day)	Gross conversion efficiency (%)	Net conversion efficiency (%)
16.1	0	28.1	-0.25 ± .04		
16.1	1.55	30.4	0.05 ± .44	3.0	4.1
16.2	2.89(3.10)+	23.6	0.47 ± .13	16.2	18.8
16.0	3.05(4.51)	26.9	0.43 ± .20	14.1	16.2
19.0	0	30.1	-0.28 ± .09		
18.9	1.45	28.9	0.26 ± .11	17.9	32.4
19.0	2.96	23.4	0.66 ± .18	22.4	28.7
19.2	4.22(4.60)	27.6	0.72 ± .26	17.1	20.2
22.0	0	31.3	-0.34 ± .07		
22.0	1.55	31.6	0.24 ± .14	15.2	36.2
22.0	3.03	28.0	0.80 ± .20	26.4	37.6
22.1	4.65	26.5	0.89 ± .23	19.2	23.8
25.0	0	31.8	-0.53 ± .09		
24.9	1.46	30.6	0.16 ± .09	11.0	44.4
24.8	3.04	31.8	0.67 ± .12	21.9	34.3
25.0	4.63	25.4	1.02 ± .23	22.0	28.9
25.1	9.11(Excess)	25.6	1.38 ± .20	15.2	17.3
28.1	0	33.4	-0.62 ± .09		
28.1	1.52	32.3	0.12 ± .07	7.8	43.7
28.0	3.08	31.1	0.65 ± .20	21.0	35.4
27.8	4.50	28.4	0.81 ± .21	17.9	24.8
28.0	10.92(Excess)	25.2	0.91 ± .21	8.3	9.4

*A summer test at low light intensity. Fish were fed live tubificid worms.

+Ration sizes in parenthesis were the prescribed ration but were not fully consumed.

a rate of 0.385%/day. Therefore, this data point was smoothed out in subsequent plots.

Growth rate was plotted against ration for each temperature (Fig. 2), resulting in curves that described maintenance ration, optimum ration, and maximum ration. These growth parameters can be derived geometrically from the

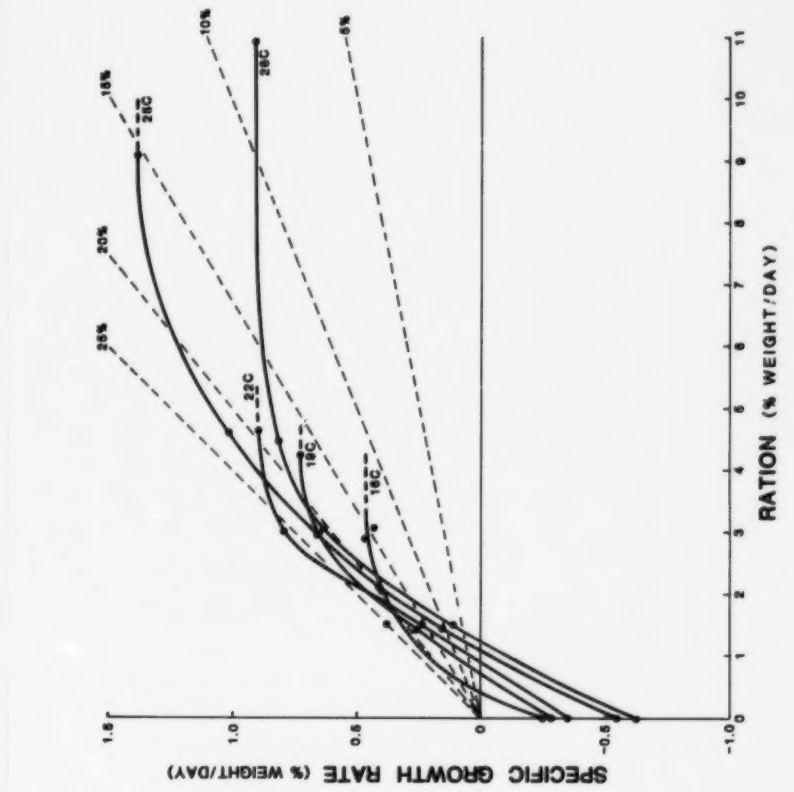

Figure 2. Relation of growth rate and ration at 5 temperatures for juvenile white suckers. Dashed lines indicate gross conversion efficiencies.

growth rate-ration size curve (Thompson 1941; Brett et al. 1969). The maintenance ration, the ration where fish maintains its weight without gain or loss, occurs where the line crosses the zero growth rate axis. The optimum ration, the ration where greatest growth occurs for the least intake, can be derived by drawing a tangent from the origin (0% growth rate and 0% ration) to the curve. The maximum ration, the ration that provides maximum growth, occurs at the asymptote of the curve.

The relation of maintenance, optimum and maximum ration to temperature

for white suckers, derived from the procedure described above, are shown in Fig. 3. The rations describing these three growth parameters increased with an increase in temperature, but both maximum ration and optimum ration decreased at temperatures higher than 25°C. At 28°C, both the maximum and optimum ration decreased due to a lower efficiency of food conversion (Table 8).

The optimum temperature for growth decreased as the ration size decreased. Growth rate was plotted against temperature for each specific ration level (Fig. 4). Each curve describes the scope for growth for fish (25-30 g) on a prescribed ration during the summer and early fall. A greater growth potential would be expected in the spring. Maximum growth rate was at 25°C on excess rations and decreased to 19°C at a 1.5% ration level. Weight loss of unfed fish increased exponentially with increased temperatures. Zero growth limits of juvenile white sucker were estimated by graphical extrapolation. Lower and upper limits were 9 and 30°C, respectively, which were similar to those observed in larvae (McCormick et al. 1977). Broken lines were drawn by eye to these graphical limits.

Gross food conversion efficiency (E_g) provides a useful index of the efficiency of white suckers to convert food into fish flesh. With a common unit of dry weight, this index was calculated using the following equation:

$$E_g = \frac{G}{I} \times 100 \qquad (3)$$

where G = growth

I = food intake

Highest conversion efficiency for each temperature occurred in the area of most rapid change in curvature (Fig. 2). The maximum gross efficiency (26%) occurred at 22°C on a restricted ration of 3.0% (Table 8). Gross efficiency was generally less than 15% at all ration levels below 16°C and at lower and higher ration levels above 25°C.

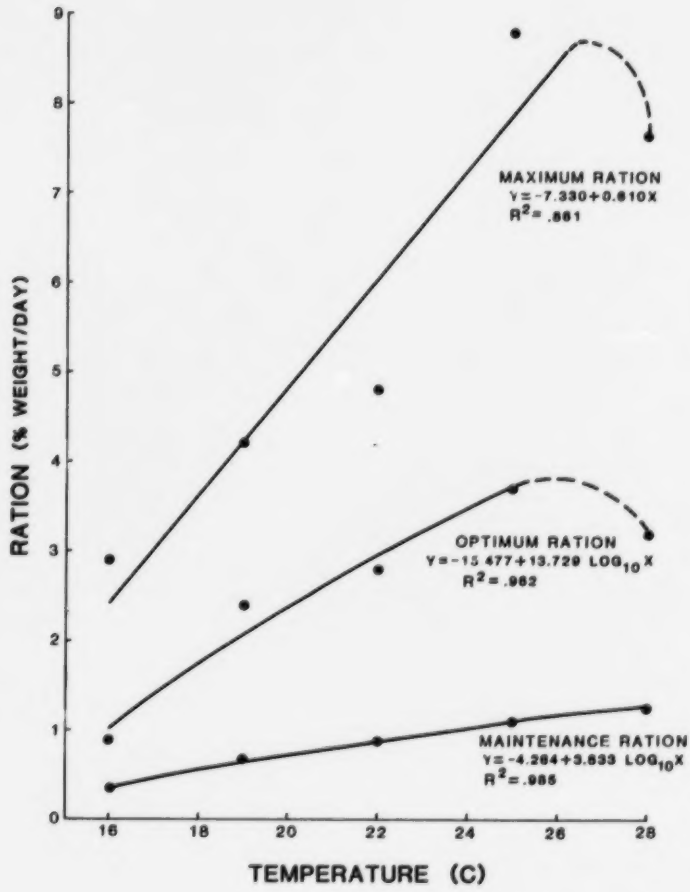

Figure 3. The relation of maintenance, optimum, and maximum rations to temperature for juvenile white suckers. Solid line fitted by regression equation, broken line fitted by eye.

The daily maintenance ration (M), obtained from Fig. 3, can be subtracted from the food intake to determine net conversion efficiency (E_n). This index measures the efficiency of utilization of the fraction of food available for growth and it can be derived with the following equation:

$$E_n = \frac{G}{I-M} \times 100 \qquad (4)$$

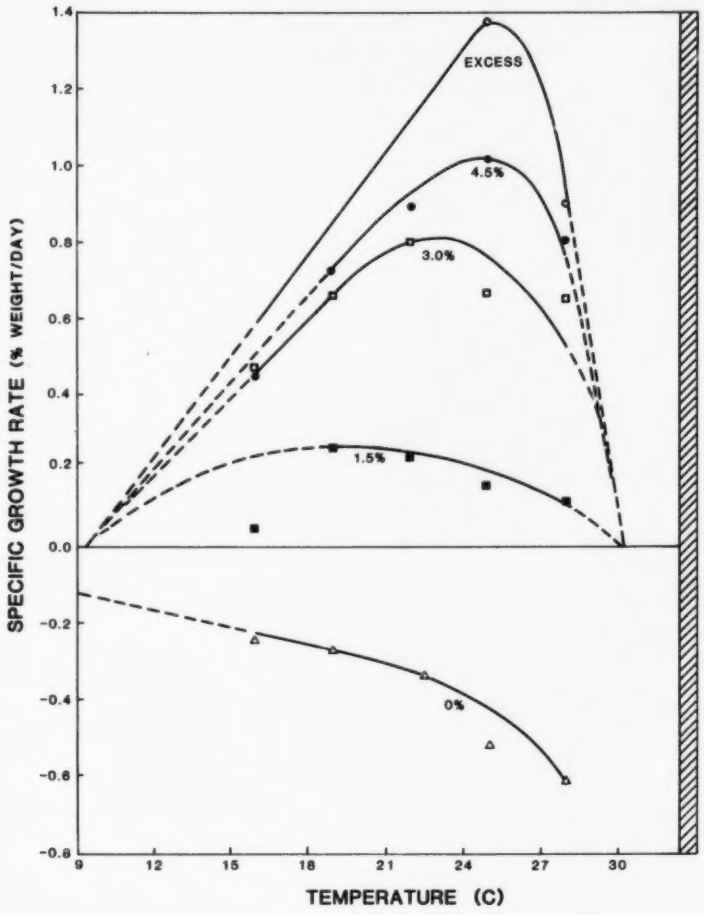

Figure 4. Temperature-growth relationships of white suckers at prescribed ration levels of live tubificids expressed as a percent of the fish dry body weight per day. Shaded area is the zone of thermal resistance in excess of the ultimate upper incipient lethal temperature of 32.5°C.

Highest net efficiency occurred at the combination of higher temperatures and lower rations. The maximum net efficiency (44.4%) occurred at a ration size of 1.46% at 25°C. In this example, the actual ration resulting in a growth rate above the maintenance level was 0.36% where fish grew at a rate of 0.160%/day.

BODY COMPOSITION

Changes in body composition were examined to determine how temperature and food intake influence the percentage of water, fat, and protein (Table 9). Samples of fish fed ration levels of live tubificids at 0, 1.5, and 3.0% were examined at the end of the test. No noticeable changes in protein and moisture contents were found between different temperatures and ration sizes. Fat content increased with an increase of food intake, particularly at temperatures of 19^{o}C and below.

Fish that showed a high growth rate during the spring were also analyzed for body composition. These fish demonstrated a much greater food intake and growth potential during this time of year. These fish were compared to fish fed a ration of 3%/day which was close to the optimum ration level for their respective temperatures (Fig. 3). No change was noted in percentage protein and water, but fat content was significantly increased over summer fish ($P < 0.05$).

TABLE 9. THE EFFECT OF TEMPERATURE, RATION, AND SEASON ON BODY CONSTITUENTS OF JUVENILE WHITE SUCKERS FED LIVE TUBIFICID WORMS*

Ration (% dry weight)	Nominal Temperature (C)	$\bar{x}$ Water+ (%)	$\bar{x}$ Fat++ (%)	$\bar{x}$ Protein++ (%)
		SUMMER FISH+++		
0.0	16	76.2	4.8	11.9
0.0	19	78.2	2.3	13.4
0.0	22	78.0	2.3	13.5
0.0	25	78.2	2.2	13.0
0.0	28	76.8	2.4	12.3
1.5	16	77.8	3.0	14.0
1.5	19	76.1	3.9	14.3
1.5	22	76.5	3.8	14.7
1.5	25	77.7	3.0	14.0
1.5	28	76.2	3.1	14.2
3.0	16	76.3	4.6	14.3
3.0	19	76.5	4.5	14.2
3.0	22	76.4	4.0	15.0
3.0	25	75.5	3.7	14.3
3.0	28	76.4	3.6	13.7
		SPRING FISH#		
Maximum	24	75.0	7.4	12.8
Maximum	26	75.7	6.0	13.4
Maximum	28	75.9	6.6	13.2

*Tubificids contained 84.5% water, 2.3% fat, and 7.4% protein.

+N = 10.

++N = 5.

+++From ration size X temperature test (Table 8).

#From season X daylength test (Table 6); initial size 10 g.

SECTION 5

FACTORS INFLUENCING SURVIVAL

For many years the standardized procedure for determining the upper lethal temperature was to subject fish to a sharp increase in temperature, usually done by a direct transfer technique from an acclimation temperature to a series of upper lethal temperatures. Many field reports have shown fish to survive temperatures higher than the reported UILT determined in laboratory studies (K.E.F. Hokanson, U.S. EPA, Monticello, MN, personal communications; Wrenn and Forsythe, 1978). It was hypothesized that the direct transfer technique under estimates the UUILT because it does not maximize the acclimation temperature and provides additional stress to the fish from handling. Theoretically, slow rates of thermal increase (< 1^{o}C/day) that maximize acclimation temperature and minimize handling stress should give the highest estimate of the UUILT.

Upper lethal temperatures were determined by both the direct transfer technique and the slow temperature rise for white suckers of different sizes (Table 10). The UUILT for smaller juveniles (19.7-34.5 g) was 32.2 to 32.5^{o}C and was 31.3 to 31.7^{o}C for larger juveniles (168-192 g) and adults. White suckers exposed to a slower rise in temperature experienced death (50%) at a temperature that is approximately 2^{o}C higher than suckers tested with the direct transfer technique and by Brett (1944), and 3^{o}C higher than the previously reported UILT by Hart (1947).

TABLE 10. UPPER LETHAL TEMPERATURES OF WHITE SUCKERS OF DIFFERENT SIZES MEASURED BY SLOW ACCLIMATION AND DIRECT TRANSFER METHODS*

$\bar{x}$ wet wt. (g)	Acclimation temperature (C)	Upper lethal temperature (C)	Source
	Ultimate Upper Incipient Lethal Temperature +		
26.7	26.1	32.4	Present study
19.7	28.0	32.2	" "
34.5	26.0	32.5	" "
30.9	28.0	32.3	" "
191.8	26.1	31.3	" "
168.7	28.0	31.7	" "
1000	23.0	31.5	" "
	Upper Incipient Lethal Temperature ++		
12-15	12.0	28.6	" "
12-15	16.1	30.3	" "
12-15	20.2	30.5	" "
12-15	24.1	30.5 (96-h)	" "
2-20	25	29.3 (133-h)	Hart, 1947
juvenile	25-26	31.2 (12-h)	Brett, 1944

*Tests conducted in summer at low light intensity

+Initial acclimation temperature increased 0.5C/day until death. Fish not handled before test as routinely done in direct transfer technique. Fish were not fed above 30°C.

++Direct transfer of fish from an acclimation tank to a series of lethal temperature baths.

SECTION 6

IMPLICATIONS FOR THERMAL CRITERIA

The physiological or growth optimum and UUILT of a species are used directly in derivation of summer limiting temperatures for aquatic life (U.S. EPA, 1976). These thermal criteria endpoints can be modified by several variables which greatly influence bioassay results and thermal responsiveness under field conditions. The light intensity threshold must be carefully controlled to provide optimal culture conditions and enhance the scope for growth for nocturnal organisms. Slower rates of temperature increase that minimize fish handling and maximize acclimation temperature give the highest UUILT. Therefore, laboratory methodology must be critically appraised before thermal criteria values are proposed or used. For some fish species, the growth optima and UUILT may be underestimated and should be revised by first recognizing sources of error as demonstrated herein.

Maximum growth of juvenile white suckers occurred over a wide temperature range of 19 to 26^{o}C, depending upon several variables. Ration level and diet quality had the greatest influence on specific growth rate and optimum temperatures, whereas season and light intensity had a lesser but significant influence on these growth responses. Body size primarily influenced maximum specific growth rate and daylength primarily influenced acclimation time to test conditions. Sucker larvae showed a similar growth response with an optimum temperature range of 23.9 to 26.9^{o}C (McCormick et al. 1979). The best culture conditions produced an optimum near 26^{o}C in this species. Lower

growth optima would most likely be observed in nature where ration size is usually restricted.

Maximum growth at optimum temperatures decreased nearly four-fold over a size range of 12 to 175 g. Optimum temperature for growth was not influenced over this fish size range. The slope for the summer maximum growth rate-body weight relationship was -0.452. The determined slope value compares favorably with salmonid growth-body weight relationships. Brett and Shelbourn (1975) found that juvenile sockeye salmon (Oncorhyncus nerka) displayed a similar slope of -0.416, but with higher intercept for a weight range of 2-40 g. Their comparison with other investigations showed that the slope value of -0.4 ± 0.04 appeared to characterize the salmonid family. The slope value declined to -0.168 by inclusion of larval white suckers in the spring growth rate-body weight relationship. This suggests that these weight correction factors are constant only for a limited size range and/or life history period.

Season had a marked effect on maximum growth of the white sucker independent of daylength changes. White sucker of a common size had a two-fold increase in maximum growth rate in spring compared to other seasons. Maximum growth rate in summer occurred at $26^{o}C$ and at $24^{o}C$ in winter and spring tests. There was no difference in growth rate between summer and winter fish under a constant 15h L-9h D photoperiod. Swift (1955) found that growth of hatchery brown trout, Salmo trutta, increased in the spring while temperatures were still cold and decreased in autumn when temperatures were still warm. These changes occurred despite the fact that they were fed to satiation. The increase in growth in the spring has been correlated with increasing daylength which stimulates endocrine activity including the production of growth hormones (STH), while decrease in growth in autumn was related to gonadal maturation (Brett 1979). Hogman (1968) also noted that seasonal changes in growth rate

of lake whitefish, Coregonus clupeaformis, was more closely related to daylength than to changes in partially controlled water temperature.

Daylength changes itself did not influence maximum growth rate or optimum temperatures in the white sucker. This is consistent with the observation that low light intensity stimulates feeding and growth in this nocturnal species. Reduced daylength, however, increased acclimation time to test conditions which has important implications in the design of "aseasonal" growth studies. Clarke et al. (1978) observed that sensitivity of salmonid fry to photoperiod varied seasonally. Gross et al. (1963) found photoperiod to affect growth of green sunfish, Lepomis cyanellus, but also noted that prior photoperiod history was important. Brett (1979) stated that for freshwater fish, that long daylength, especially increasing daylength applied over a number of months in the right season, is stimulating to growth. The observed effects on growth are not large. Decreasing daylengths have an inhibiting effect on some freshwater fish. Growth of nocturnal species such as walleye, Stizostedion vitreum, is relatively more temperature dependent, while growth of diurnal species such as yellow perch, Perca flavescens, is relatively more photoperiod-dependent (Huh et al. 1976). The lack of greater induced response by photoperiod, compared with natural seasonal effects on normal populations (independent of temperature effects), suggests the evidence for an endogenous annual rhythm which is not subject to displacement by artificial control of daylength.

The loss of condition of winter fish and endogenous hormonal cycles may stimulate increased feeding to restore body food reserves. The growth rate of white sucker increased in spring due to a large increase in food consumption. Starvation alone is a normal endogenous stimulus to feeding activity. Therefore, it is possible for suckers to increase their growth rate without appreciable changes in food conversion efficiency or even with a possible

decrease in efficiency. Wurtsbaugh and Davis (1977) indicated that rainbow trout, Salmo gairdneri, were less efficient in food utilization for growth in the spring. The increased growth in spring in suckers, consisted of a large increase in relative fat content compared to other seasons. Fat deposition of accumulation can occur rapidly in fish in response to enhanced feeding activity, and can also be rapidly depleted on demand by other metabolic processes and by overwintering (Shulman 1974). Although no fat analyses were done on fish prior to testing, it was observed that fish at this time of year were in relatively poorer condition at the start of the study than at other times of the year.

The specific growth rate of the white sucker of a given size and season is dependent mainly on the quantity of food consumed and temperature. Increasing temperatures markedly increased the maximum ration, optimum ration, and maintenance ration, but at temperatures above 26°C, both the optimum ration and maximum ration decreased. This decrease was probably due to a lack of appetite and the increase in maintenance requirements, and lower food conversion efficiency. Maximum gross food conversion efficiency for white suckers was 26% at 22°C and 3% ration level which compares favorably with salmonids. Increasing temperatures also reduced gross efficiencies at low ration levels (1.5%), while little effect was noted at higher ration levels. This pattern was also found for rainbow trout (Wurtsbaugh and Davis 1977) and for sockeye salmon (Brett et al. 1969).

Slow increases in temperature that maximize acclimation temperature without handling fish has significantly increased previous estimates of the UUILT. Juvenile and adult suckers tolerated temperatures 32.5° and 31.5°C, respectively. The UILT for juvenile white suckers in this 96-h summer test was 30.5°C. Brett (1944) reported an UILT of 31.2°C in a shorter 12-h

summer test. A time period of at least 72-h is required to measure an UILT (Brett 1970). Hart (1947) measured an UILT of 29.3°C for juvenile suckers acclimated to 25°C in a winter test. The UILT of newly hatched and free-swimming larvae were 28.2 and 30.5°C, respectively (McCormick et al. 1977). These previously reported limits were based on tests where fish were subjected to a very quick temperature change. When fish were exposed to a slower temperature increase, an UUILT endpoint that was 2-3°C higher than the UILT was attained for juvenile fish. This method avoids handling stress and maximizes acclimation temperature. This method gives a more realistic upper lethal limit when compared to field situations where fish have been observed at temperatures higher than the upper lethal temperatures previously reported in the literature.

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